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Northwest Atlantic Fisheries Organization

Serial No. N1281

NAFO SCR Doc. 87/12
(revised)

SCIENTIFIC COUNCIL MEETING - JUNE 1987

Understanding Marine Fish Communities: Historical Perspectives, Recent Research, and Future Directions

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Introduction

An examination of the current fisheries and ecological literature will reveal a wide variety of investigations focusing on structuring factors of fish communities. At the present time, ecologists are debating the importance of relatively deterministic biotic interactions as factors that limit the distribution and abundance of marine organisms in general and fishes in particular. The literature generated from these diverse investigations revolves around the concept of competitive interactions for limiting resources, which structured communities of organisms. Some studies provide supportive data, while in others, evidence is often circumstantial, contradictory, or lacking. The time seems right, then, to review the history of community studies in terms of concepts, the direction current research is taking (or if there is direction), and prospects for future investigations.

The objectives of the review will be to:

1. examine the historical progression of community studies (in terms of direction these studies have driven subsequent research).
2. examine the scaler levels and methodological factors in studies which had diametrically opposed conclusions in communities.
3. determine if methodologies are properly derived to measure the required parameters.

4. determine if we are selectively collecting evidence to support (incomplete) theories (or, if our underlying assumptions regarding competitive interactions structuring communities are correct), and
5. determine if we reached a level of greater understanding of the ecological concepts of the interactions (e.g. competition, coexistence) structuring animal communities (fish communities in particular) from original concepts to the present.

HISTORICAL PERSPECTIVE

Although the concepts of community structure are relatively recent in the history of science, scientists and naturalists have been examining living and fossil species, sympatrically distributed (i.e. living in communities), through the lower Cambrian. This time could be pushed back further to include unicellular organisms to approximately 3.8 billion years BP. Biologists from the late nineteenth and early twentieth centuries had data suggesting some type of underlying principle which structured assemblages of organisms (Steere, 1894; Grinnell, 1904). Mathematical models were then developed which demonstrated that for pairs of species utilizing a finite required resource, the availability of the resource limited population size (Haldane, 1924; Lotka, 1932) and if continued through time, maintaining competition, one species population would become extinct. Experiments such as those by Gause et al. (1934) provided evidence that the simple model predictions were accurate, at least under laboratory conditions. Gause (1934) took Malthusian population theory and applied it to the next greater level of ecological complexity - the community. This neo-Malthusian theory is based on a deterministic density-dependent population model based upon resources. Gause (and much later Hardin, 1960) also defined the concept of the niche, more exactly such that species do not occupy exactly the same niche space but exhibit some displacement along certain resource axes where some species would have a competitive advantage over all other species.

Basic or textbook community theory is essentially based on assumptions that as populations grow, resources are depleted to a point where resource shortages produce competitive interactions between and within species. That is, competition is a density-dependent phenomenon. With this theory in hand, biologists set about collecting data supporting this neo-Malthusian theory. They were able to collect data on community structure and interpreted the structure to be the causal result of competitive interactions (Hutchinson, 1959).

The time frame of these interactions then became of interest. Interpretation of the concept of the niche leads to the inference that speciation events were caused by competition between diverging populations, and the species which comprise present communities are the result (Schoener, 1974). The point being that one can sample a community, determine the niches of each of the component species along one or several resource axes, and assume that competition keeps each species in a well-defined niche. The next step in this argument, however, is providing proof of present or ongoing competitive interactions, or are the data on resource partitioning the result of morphological and behavioral limitations imposed by historic speciation events (Connell, 1980). Biologists are now examining diverse types of communities to determine whether competition is a structuring force or remnant interaction (see Strong et al. 1984 for an extensive review and current problematical discussion).

Is there a compromise view? Do any communities exist at levels where component populations remain at low densities so competitive interactions do not determine structure and only exhibit competitive mediation occasionally when populations increase? Interactions would limit further increases and populations would rebound down again to non-competitive levels.

The working hypothesis of many recent community studies centers on the role of competition as a cause of pattern in resource utilization, distribution, and relative abundance of an animal species. Tests for competition are often indirect (e.g. removal experiments, comparisons of resource utilization of two species where distributions do not overlap), yielding data with patterns consistent with competition theory but with other possible explanations.

Direct tests are difficult and of undetermined value because they require reductionist tactics, since communities and their resources are not amenable to direct manipulation. This tactic of examining communities also requires the investigator to look at only a few species when communities require a "holistic" approach. The recent literature is full of requests for hypothesis testing of competition with direct field experiments (Connell, 1974, 1975; Wiens, 1977; and others).

Finally, with these types of data, ecologists look for recurrent, predictable patterns with which to construct community models. Accurate models would be of great use to resource managers and ecologists in general; the reasons are obvious. However, communities with similar phyletic components may behave similarly while communities from different geographic regions or with different structuring factors will not behave like models of other communities. At present, no such models exist.

Marine Fish Community Studies

The aim of community studies is to find patterns in the structure of groups of organisms. Marine fish communities provide interesting and globally widespread examples of dynamic community processes. Evolutionarily, fish communities are older than terrestrial systems, and knowledge of community processes will aid our general understanding of community systems evolution. Practically, marine fish communities are generally exploited for food resources by man, and an understanding of how they function may allow optimal plans for utilization and production.

The following sections present literature reviews of our current state of knowledge of marine fish community systems and dynamics. Within this review are discussions of problems inherent to different approaches and how results fit into our current level of understanding.

- Tropical Systems

The study of tropical marine reef fish communities is a relatively recent endeavor when compared to other aquatic and terrestrial systems. Bardach (1959) and Randall (1961, 1963, 1965) began pioneering studies of reef fish as ecological groupings and examined the role of habitat and environment on community structure.

At the time these early marine investigations were in progress, studies in other areas had already hypothesized the types of patterns which would exist in tropical environments. The predicted patterns were based on the working hypothesis that tropical systems were highly diverse, equilibrial in nature, and competitively organized; the diversity being achieved by narrow partitioning or high overlap of resources by component species (MacArthur, 1965, 1969; Paine, 1966; Pianka, 1966; and others).

Odum and Odum (1955) and Hiatt and Strasburg (1960) described the ecosystem at Eniwetok Atoll in the South Pacific as a stable, equilibrium system with a biotic component which is competitively structured under constant environmental conditions. The same conclusions were drawn from more recent work (Gladfelter and Gladfelter, 1978; Molles, 1978; Smith, 1978).

Searching for underlying mechanisms for these apparent patterns, investigators developed hypotheses to explain them, such as stability-time (Sanders, 1969) and predator mediated co-existence (Paine, 1966).

Future studies elucidated aspects of competitive structuring mechanisms through resource limitation and partitioning. No evidence is presented in the literature which demonstrates food resources are limiting tropical reef fish populations. Tropical fishes have specialized species-specific space resource requirements, hence space resources are a probable limiting factor of fish populations. (Ebersole, 1977; Gladfelter and Gladfelter, 1978; Low, 1971; Luckhurst and Luckhurst, 1978; Sale, 1977; Shulman, 1985; Smith and Tyler, 1972; and others).

Problems of scale begin to appear in these space resource studies. Sale (1972) showed that the numbers of the pomacentrid Dascyllus aruanus on isolated coral heads, were highly correlated with coral size (indicating space resource limitations). At other larger sites on the reef proper, which had no limitation of coral, no correlation was found.

Smith and Tyler (1975) showed that there was significant seasonal variation in the numbers of fish on a patch reef off Bimimi, Bahamas. Sale (1984) argues that this variation indicates space resources are not limiting throughout the year. This is only one explanation of the variation, however, as spatial requirements of individuals within species change on a temporal basis (i.e. with growth of individuals, during breeding). The variation in numbers may then reflect intense competition for more space (or greater defense of the same territory), causing individuals to leave the patch reef for other areas. Other long-term studies of natural and artificial reefs have yielded similar results (Russell et al., 1974; Talbot et al., 1978; Bohnsack and Talbot, 1980; Williams, 1980). Without knowing the behavior of individual components of the system and the reason for emmigration, it is not reasonable to assign causal relationships to the observations. For example, Shulman (1985) found temporal scales for aggressive defense of nocturnal shelter sites in the range of hours. This effects, on the very short-term, the number of individuals (and probably species) utilizing near-field spatial resources.

Through these observations, two schools of thought have developed regarding the structuring of reef fish communities. There is the theory of determinism (order) of fish community structure (Smith, 1977, 1978; Helfman, 1978) based on observations of constancy of composition over time. In this theory, fishes have narrow species-specific habitat requirements which reduce competitive interactions resulting in a deterministic community structure based on habitat. Alternatively, there is a theory which embraces a diametrically opposed viewpoint which describes the stochasticity (chaos or lottery) of fish communities on reefs (Sale, 1978; Talbot et al., 1978). In this theory, the unpredictability of fish community composition is attributed to factors (such as predation, death) creating ephemeral openings of spatial resources. Colonizers (individuals or species) are recruited by chance processes, although, some priority effects by residents affecting new recruits have been discerned (Shulman et al., 1983). Hence, unpredictable does not necessarily mean chaos.

Bohnsack (1983) enumerated the species turnover rates on artificial and natural coral heads. He suggests that understanding turnover, central to the MacArthur-Wilson island biogeography model (MacArthur and Wilson, 1967), may reconcile differences between the two fish community theories. He found the rate and length of time of sampling greatly effected perceptions of community changes. The order theory proponents had sampling intervals of one (i.e. Smith and Tyler, 1972, 1973) to thirteen years (i.e. Ogden and Ebersole, 1981), while the chaos theory proponents sampled at much shorter time scales (monthly to quarterly) (Talbot et al., 1978; Sale, 1975, 1978; Sale and Dybdahl, 1975). Therefore, the controversy may have originated in part as an experimental artifact caused by turnover rate and differences in sampling interval. Island biogeographic theory may explain these differences, and data suggests patch reef fish communities are in "dynamic" equilibrium.

What of large scale contiguous reefs? Williams (1982) and Anderson et al. (1981) found significant differences in the composition of fish communities, within selected families, at different zones across the Great Barrier Reef. Differences between major zones across the shelf were much greater than replicates within reefs. These differences may be attributed to, in terms of community theory, a compromise view of the chaos versus order theories described by Smith (1978). The fish fauna on any reef is the result of a mult-tiered screening process of the regional fauna. The first screen limits recruits by physico-chemical constraints (i.e. inappropraite microhabitats). The second screen, being random events, limiting recruitment such as non-selective predation on recruting larvae or transformed juveniles and transport of larval recruits by currents. The third and final screen, being a selective recruitment process, involves inter- and intraspecific competition for space or food and species-specific symbiotic relationships.

Smith (1978) suggests that another perspective of this same compromise view "is to consider that the local community is made up of a small number of species selected partly randomly and partly deterministically from the regional faunal pool. Only a limited number of species can occur together in a small patch of habitat, but if there are enough patches, a very large fauna can be accommodated. Because of the random effects of the selective process, similar habitat complexes may have quite different faunas that are no less stable." Since successful recruits probably do notoften change residence on the reef, these individuals have priority over potential recruits. As older fish die or are removed by predation, new recruits will take their place. There is a constant turnover but species number remains relatively constant.

Each theory retains its proponents. Present studies on methodological comparisons (i.e. Bohnsack, 1983), recruitment patterns (i.e. Shulman et al., 1983), and discussions of differences in workable theories (i.e. Helfman, 1978; Sale, 1978, 1984; Smith 1978), create an information pool which is narrowing in on assembly rules (Diamond, 1975) of coral reef fish communities. It may be, then, that the reef fish community is more than the sum of its parts. That is, larger scale reef tracts have emergent properties not exhibited by small, isolated coral heads and finer scale observations of larger areas would be required to understand limiting factors that are not continuous. Factors such as agonistic interactions influencing recruitment and shelter occupancy (Shulman et al., 1983, Shulman, 1985), territoriality (Ebersole, 1977), and small-scale habitat changes (Gladfelter and Gladfelter, 1978). Although we have developed the ability to perform hypothesis testing experiments on small reef tracks, or coral heads, we must develop methodologies to perform replicate sampling over large reef tracks and elucidate the scale at which these enumerations are significant.

- Temporate/Boreal Systems

Studies of temperate and boreal fish communities have generally taken a different tact in perspective. While studies of tropical reef fishes generally take a small-scale perspective (in-situ approach), studies of temperate/boreal fish fauna have generally (historically) utilized large-scale sampling techniques (trawl catches) over wide geographic areas (i.e. Overholtz, 1982).

Although one rationale for this dichotomy of scaler approaches is that (1) coral reef fishes generally have limited home ranges and live in a complex three-dimensional habitat amenable to small-scale census techniques, and (2) temperate/boreal fishes are generally more spatially dispersed, exhibit seasonal migration (inshore-offshore or alongshore), and live in turbid, less spatially complex environments amenable to large-scale census techniques. Interactions which define competitive interactions or allow co-existence, however, still occur at the level of the individual.

Studies of tropical reef fishes have focused on the aspects of space resources and interactions limiting access to space resources as the structuring factor in these communities. Most studies in temperate and boreal waters have focused on food resource limitation as a structuring factor.

Food habits of dominant shelf fishes change with size (Tyler, 1972; Ross, 1978; Langton and Bowman, 1980; Lilly and Fleming, 1981; Sedberry, 1983). As growth occurred, predators were found to switch to different, larger prey taxa. Total volume of prey increased with increased fish length. Many predators fed on increasing numbers of similarly sized small food items, up to a certain length. This strategy maximized energy intake for growth and reproduction.

Schoener (1971), using optimal foraging models, predicted that food size would decrease with decreasing predator size, and do so asymptotically. Many studies demonstrate this prediction (i.e. Hacunda, 1981) while others (i.e. Lilly and Fleming, 1981; Sedberry, 1983) indicate that predators in a specific feeding stanza prey on organisms over a set size range throughout a wide growth phase, or, as a predator size increases, the size of prey expands as well, retaining small prey in the diet. Juvenile and adult shelf fishes off the U.S. coast of the northwest Atlantic show considerable interspecific overlap in diet, with interspecific, functionally similar groups of predators feeding on a few principal prey species (although some species-specific selectivity is evident at some points in time).

Optimal foraging theory predicts that as food becomes scarce, predators will take a wide variety of prey, and the diets of functionally similar predators occupying the same habitat will converge (Pyke et al., 1977). Some authors (i.e. Tyler, 1972 for Passamaquoddy Bay; Jones, 1978 for the North Sea) have hypothesized that as food density declines, co-existing predators will specialize on differing prey, hence, decreasing overlap. Considerable food overlap would occur only if prey were abundant. Ross (1977) found that interspecific food overlap in co-occurring sea robin species (Triglidae) was at a minimum during periods of low prey availability, thus supporting the latter hypothesis. Tyler (1972) found little overlap in principal prey species of a boreal marine fish community off Atlantic Canada and concluded that specialization of prey resources is a result of a food limited system. Conversely, Sedberry (1983) found overlap lowest in spring when food resources were most abundant.

The results of these studies leave the question of whether this overlap is due to food resource limitation or surplus. Also, there is still the underlying question of whether there is competition for food resources among fishes in these temperate/boreal communities, and is this, in part or in total, what structures the community as a whole? Although shelf fishes exhibit interspecific diet overlap, this condition does not necessarily lead to competition unless resources are limiting (Pinaka, 1976). Other factors need to be considered such as small-scale distribution and interactions between predators and between predators and prey.

Unlike relatively (temporally) stable tropical coral reef fish communities, temperatre and boreal fish communities generally exhibit some large-scale (seasonal) temporal variability. For example, in the northwest Atlantic, fish communities north and south of Cape Cod show distinct differences in species composition related to seasonal differences in water temperature (Colton, 1972; Colton et al., 1979).

Breaking each community into temporally scaled parts, it is possible to separate the component species into year-round residents, winter residents, summer residents, and occasional species (Tyler, 1971). Areas with narrow temperature fluctuations (i.e. boreal communities north of Cape Cod) were dominated by year-round residents. Areas exhibiting greater annual temperature fluctuations (south of Cape Cod) had more temporary residents, and fewer year-round species (even boreal resident species exhibit inshore-offshore or shallow to deepwater movements on diel and seasonal scales).

Recksiek and McCleave (1973), working in the Sheepscot River-Back River estuary at Wiscasset, Maine, found pelagic fish communities corresponding to Tyler's community structure groupings. The relatively warm Back River estuary had a summer pelagic component consisting mostly of alewives (Alosa psuedoharengus), blueback herring (Alosa aestivalis), and Atlantic menhaden (Brevoortia tyrannus), while the relatively colder and oceanic Sheepscot River estuary had a summer migrant pelagic component of Atlantic herring (Clupea harengus), Atlantic mackeral (Scomber scombrus), and spiny dogfish (Squalus acanthias). Rainbow smelt (Osmerus mordax) was the only year-round resident, and Atlantic herring was the only winter resident species. It appears, therefore, that although pelagic and demersal fish assemblages can be divided into similar residency patterns, species composition varies with temperature regime, both within and between latitudes in these temperate and boreal systems.

At even smaller scales, other types of distribution factors, such as movements and interactions of predators, come into play. Most of what is known about temperate and boreal fish communities comes from remote trawl survey methodology. Problems of selectivity of the fishing gear give a biased sample of species composition and abundance due to species and size specific avoidance (Byrne et al., 1981). Comparisons of one survey tow to another, in community studies, makes the implicit assumption that the fish are homogeneously distributed over the tow area and all fish are interacting. Also, when comparing tow caught fish within and between tows for overlap in diet, the implicit assumption is made that the fish all forage within the same prey pool. A submersible transect over a known trawl area on Jeffreys Ledge, Gulf of Maine, revealed habitat partitioning (rock-boulder versus cobble-sand) of several species (e.g. redfish, Sebastes marinus; cunner, Tautogolabrus adspersus; eel pout, Macrozoarces americanus; longhorn sculpin, Myoxocephalus octodecemspinosus), demonstrating small-scale spatial discontinuities of species distributions (Auster, unpublished data). In addition, factors affecting the prey pool available to individual predators are little understood. Fish feeding in significant currents on planktonic prey have been observed to feed only in an upcurrent direction (Auster 1985a). Depending upon the size of planktonic prey patches and the position of individual predators within the prey field, the possibility of downfield depletion exists. Consumptive competition (sensu Schoener, 1983) may be common in current dominanted environments. Fish use currents in a way which isolates individuals by size class for short periods in order to take advantage of "current sheltered" prey pools in current dominated environments (Auster, 1984, 1985b). Cylical changes in tidal current velocity shift the small-scale spatial distribution and change foraging behavior patterns of fish by species and size class. For example, increasing current velocity allowed only increasingly larger size classes of cunner to forage on current exposed surfaces and restricted the head raised searching posture of winter flounder (Psuedopleuronectes americanus) to only those size classes capable of maintaining this position above (rather than with all distal fin rays on) the substrate. Size class groups within a species are limited in their maneuverability at specific current velocity regimes. Areas exposed to currents limited the foraging behaviors of each species by size class and became ephemeral prey refuges from specific size class fish as current velocity increased. Changes in distribution and behavior continuously shift the potential foraging areas (and prey pool) for each species-size class group. This phenomenon may provide an isolating mechanism to reduce both inter- and intraspecific competition in a food limited system.

Groups of fishes within communities also switch into prey pools unavailable to other species when these alternate prey become available. For example, seasonal food overlap values for demersal shelf fishes in the Mid-Atlantic Bight were lowest during spring, when a high abundance of planktonic prey was available nearbottom. The normally benthic predators, red hake (Urophycis chuss) and Gulf Stream flounder (Citharichthys arctifrons) switched to planktonic prey (Sedberry, 1983). On a shorter temporal scale, Pearcy et al. (1984) reports that adult ocean sockeye (Oncorhynchus nerka), pink (O. gorbuscha), and coho salmon (O. kisutch) switch to euphausiids at night, from squid, fish and amphipods during the day. Chum salmon (O. keta) feed at all times, generally on salps, with little diel shift. These shifts suggest that salmon are opportunistic and able to exploit food resources when they are encountered. These examples of prey switching suggest that fish whose functional morphology allows exploitation of an opportunistic resource will do so, hence reducing pressure on the other common prey pools.

The previous examples of studies at different scaler levels suggest, that in most of the flat, trawlable shelf areas where we have a familiarity of the community of semi-migratory to migratory fish, we are still in the process of identifying factors that may aid in structuring communities. There are groups of fish that have limited home ranges and specific small-scale habitat requirements (like rock reefs). The few studies of these groups in temperate/boreal systems suggest they may behave somewhat like tropical reef systems.

Gascon and Miller (1981) studied the development of fish assemblages on artificial reefs in the nearshore environment of British Columbia, Canada, using small-scale visual census techniques. Species equilibrium in all cases was reached within 6 months. Assemblages were more stable and predictable than patterns found in several recolonization studies in tropical systems. (Russell et al., 1974; Sale and Dybdahl, 1975; Sale, 1977, 1978; Talbot et al., 1978). The authors suggest that the observed stability is a result of a smaller pool of potential colonizers (30 species), as opposed to many more in tropical systems (105 species reported by Talbot et al., 1978). No competitive interactions were reported in this study although winter and summer insular reefs were significantly different. The non-equilibrium (lottery) model of Sale (1977, 1978) may apply in this case although Helfman (1978) suggests that the species pool available for colonization is a major factor controlling similarity between reef systems.

Ebeling et al. (1980) also found the same type of patterns in temperate kelp bed fishes off California. This study compared canopy and bottom fish assemblages at an inshore and offshore site from annual surveys, between 1971 and 1974. Variation in species composition (stability) was less between years than between habitats or sites. Site- and habitat-specific species composition persisted although there was significant yearly variation in species abundances. Canopy assemblages, dominated by planktivores (a low number of potential species), were simpler and more variable than bottom assemblages.

These studies suggest that there is some "optimal" or "critical" species pool to draw on for colonizers where community stability would persist. Below some level, communities are less stable and subject to large variations in composition and number. The canopy fish community in Ebeling et al. (1980) drew on the smallest potential species pool and exhibited the greatest variation. However, the kelp canopy is an ephemeral environment subject to variable primary production, storm breakage, and planktonic prey abundance. This habitat is in itself less stable than demersal habitats (rock-boulder reefs, kelp holdfast and lower blade habitat). The variability of the habitats themselves and their associated "attractiveness" to potential colonizers could contribute to a great deal of the variability of species composition and abundance.

Rockfishes (Sebastes spp.) of the family Scorpaenidae are an interesting group to examine for the effects of resource partitioning and competition in temperate/boreal environments. The genus contains 100 species reported from the North Pacific (69 species in the eastern North Pacific). As many as 50 species occur in a narrow latitudinal band (34° - 38° N) off central California (Chen 1971, 1975). Many cogeners are morphologically similar and co-occur in a variety of habitats, hence the potential for competition and overlap is high (Larson, 1980).

Evidence of direct competition between rockfish cogeners has been reported by Larson (1980) and Hallacher and Roberts (1985). Rockfish cogeners exhibited species-specific spatial zonation in kelp bed habitats, with the exception of several spatial generalists. Food habits reflected the prey pool available in the spatial zones occupied, hence overlap did not signify direct competition for prey resources. Manipulative field experiments by Larson (1980) have demonstrated small-scale range extensions into a cogeners habitat when the cogener is removed, indicating interspecific competition. The segregation was found to have originated by selective settlement of larvae and maintained by interspecific territoriality.

Segregation to avoid direct competition for food also occurs within habitats by diel partitioning of activity and use of spatial resources (e.g. shelter sites, foraging sites) as in tropical systems. For example, on nearshore rocky reefs off southern New England, there are distinct changes in diurnal and nocturnal fish community structure and activity (Auster, unpublished data). Cunner are typical scan-and-pick feeders during the day but are inactive at night (Olla et al., 1975; Sand, 1982). Other species, such as hake (Urophycis spp.) and scup (Stenotomus chrysops), move into the area at night for shelter and to forage. Rock gunnel (Pholis gunnellus), shanney (Ulvaria subbifurcata), and grubby sculpin (Myoxocephalus anaeus) move out and away from the reef habitat to forage on adjacent sand or mud areas.

Despite the variability exhibited by many communities examined at widely disparate scales, temperate/boreal assemblages also are stable in structure over the course of years (Ebeling et al., 1980; Overholtz, 1982). In highly perturbed systems (i.e. high fishing mortality) there have been community responses in which species composition and abundances have shifted to new equilibrium levels. In the northwest Atlantic, there has been a dramatic increase in sand lance (Ammodytes spp.) populations (Sherman et al., 1981) as a hypothesized response to depletion of herring and mackeral stocks. Exploitable fish biomass in total was reduced approximately 50% from 1978 to 1975 (Clark and Brown, 1977). Also, in the North Sea it has been hypothesized that high fishing mortality of herring and mackeral stocks during the 1970's is responsible for their replacement by large populations of small, fast-growing, opportunistic plantivorous species (e.g. pollock, sand eel, and eel pout) (Andersen and Ursin, 1978). This replacement phenomenon is similar to the results from tropical reef fish studies showing replacement of species (individuals) on patch reefs, where these niches are refilled by trophically similar species. The resilience of the communities as a system, rapidly moving to new states of equilibrium, demonstrates how complex

systems restore components to maximize energy flow.

Studies of other taxa suggest environmental variability is responsible for the coexistence of species communities (e.g. Dayton, 1971; Caswell, 1978). Hence, destabilizing environmental parameters (e.g. aperiodic high velocity currents, wide temperature fluctuations, fluctuations in salinity, etc.) may also be responsible for coexistence of species of fish communities as well (Thorman and Wiederholm, 1983). The coexistence of species in various communities may then be the result of some combination of isolation and instability factors working in concert to reduce or eliminate competitive interactions.

Current and Future Perspectives

The preceeding review of the fish community literature demonstrates the diverse temporal and spatial perspectives that biologists have used to elucidate the functional aspects of community structure. Opposing viewpoints on basic stochastic versus deterministic structuring of communities are widespread in the literature, although studies like Bohnsack (1983) and Shulman et al. (1983) are beginning to look at finer scale effects to discern why such divergent conclusions regarding structuring roles could be drawn from essentially similar communities.

Problems regarding our understanding of many scaler processes are promulgated by viewpoints transcending hierarchical divisions (e.g. interpreting small-scale processes through large-scale views and vice versa). For example, competitive interactions between and within species are often inferred from remote trawl sampling (at various temporal and spatial scales) without regard to small-scale distribution and behavior, the scale at which these interactions would occur.

The underlying questions of this review are: do we understand fish communities any better today than we have in the past, and are we headed in the right direction? In terms of understanding and direction, we have begun to refine the types of questions we are asking, from general to specific, and elucidate patterns of community structure and dynamics caused by multiple variables. This has only been done in a few cases, but we seem to be on track. We are not yet at the stage where predictive modeling is proposed or even a reasonable endeavor due to a lack of data on any "entire" community overall. In particular, there is a lack of data regarding recruitment of fish from the plankton and how they enter the community structure. This is true for all regions.

As present work progresses and future studies ask even more refined questions, community dynamics will be "mapped" to provide data for predictive modeling. Once this task is possible, management strategies could be tested and best options chosen for optimal utilization of fishing resources. This information will also enhance our general understanding of processes governing community evolution.

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